

PSYCHE

Vol. 85

December, 1978

No. 4

TERGAL AND STERNAL GLANDS IN ANTS*

BY BERT HÖLLDOBLER AND HILTRUD ENGEL

Department of Biology
MCZ Laboratories, Harvard University
Cambridge, Massachusetts

INTRODUCTION

Chemical signals, or pheromones as they are generally called, play a central role in the complex communication system of ant societies. During the last 20 years a number of exocrine glands have been identified as the anatomical sources for a diversity of pheromones which mediate sexual and social behavior in ants (for reviews see Wilson 1971, Blum 1977, Hölldobler 1978).

In recent years, however, several hitherto unknown exocrine glandular structures have been discovered in ants and the behavioral functions of some of them have already been determined. In this paper we will review these findings and will report the new results of our comparative morphological study of tergal and sternal glands in ants.

MATERIAL AND METHODS

For histological investigations live specimens were fixed in alcoholic Bouin (Dubosqu Brasil) or Carnoy (Romeis 1948), embedded in methyl methacrylate, and sectioned 8μ thick with a Jung Tetrander I microtome (Rathmayer 1962). The staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A Scanning Electron Microscope. For some of the species which could only be identified to the generic level, the respective number is given of the voucher specimens, which are deposited in the ant collection of the MCZ (Harvard University).

*Manuscript received by the editor May 3, 1979.

RESULTS

Tergal glands

a. Pygidial gland

In a detailed anatomical study of *Myrmica rubra* Janet (1898) described a pair of clusters of a few glandular cells, located under the third gastric tergum. Each cell sends a duct through the intersegmental membrane between the third and fourth gastral terga. We discovered a similar, but considerably larger paired glandular complex at the same anatomical position in *Novomessor cockerelli* and *N. albisetosus* (Hölldobler et al 1976). Kugler (1978) recently investigated a number of myrmicine ants and in many of them he found the gland, which had "distinct reservoirs, produced by invagination of the intersegmental membrane between abdominal tergum 6 and tergum 7 (pygidium)". Kugler suggested that these glandular organs be called *pygidial glands*. We accept this terminology, because it describes the anatomical designation of the organ more precisely than the term "dorsal gland" or "tergal gland", originally suggested (Hölldobler et al 1976, Hölldobler and Haskins 1977). However, it has to be pointed out that the pygidium of the ants (the last exposed tergum) is the 7th abdominal tergum and is not homologous to the pygidium of the Coleoptera (8th abdominal tergum). Hence, the pygidial glands of ants are not homologous to the pygidial glands of Coleoptera.

In a previous study (Hölldobler and Haskins 1977) we found pygidial glands with large reservoirs in several ponerine and myrmeciine ants (*Amblyopone*, *Paraponera*, *Ectatomma*, *Odontomachus*, *Pachycondyla*, *Platythyrea*, *Rhytidoponera*, *Myrmecia*) and we demonstrated that the virgin females of *Rhytidoponera metallica* attract males by the release of a pheromone from these glands. In his anatomical studies of *Rhytidoponera metallica* and *R. convexa*, Whelden (1957, 1960) described a pair of cell clusters each comprising 8–15 glandular cells. Each cell sends a duct through the membrane connecting the 6th and 7th abdominal segments. We are now certain that Whelden already had discovered the pygidial gland in *Rhytidoponera*; his histological methods, however, may not have enabled him to detect the large reservoirs associated with the glandular cell clusters. Similar paired glandular structures were found by Whelden (1957) in the ponerine species *Stigmatomma* (= *Amblyopone*) *pallipes*.

Finally, independently of our investigations, Maschwitz (pers. communication) found a pygidial gland in *Leptogenys chinensis*, which he called the "dorsal gland" (Maschwitz and Schönege, 1977).

The new anatomical investigations presented in this paper reveal that the pygidial glands are much more common in ants than previously assumed. Usually the organ consists of a pair of lateral clusters of glandular cells, each cell sending a duct through the intersegmental membrane between the 6th and 7th abdominal terga. Depending on the species, the intersegmental membrane can be invaginated to different degrees, so that it can form a more or less voluminous reservoir (Fig. 1, 2, 3, 4). If no reservoir is present, the glandular structures can easily be missed during the dissection and histological sectionings are therefore required to determine whether or not the pygidial gland is present. As we have already indicated for *Novomessor* and as confirmed by Kugler (1978) for several other myrmicine species, the pygidial gland can be associated with a special cuticular structure on the pygidium (7th tergum), (Fig. 5, 6, 7). Our histological studies demonstrated, however, that the absence of such structures does not necessarily indicate the absence of

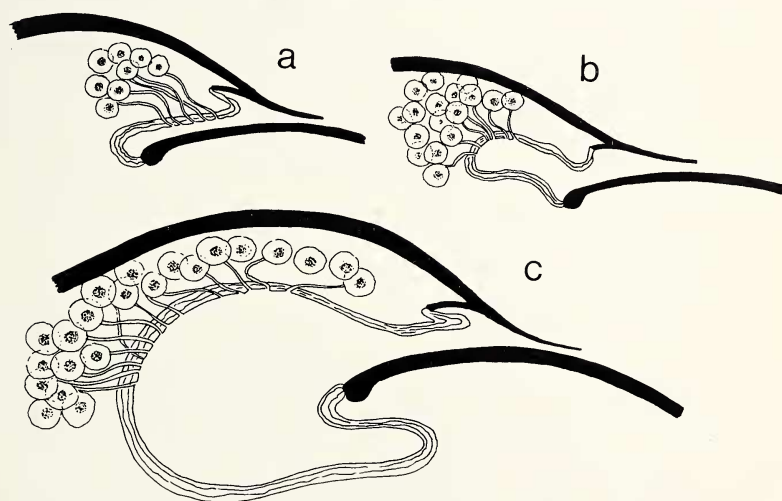


Figure 1. Schematic illustration of glandular cells that send ducts through the intersegmental membrane. When the membrane is increasingly more invaginated, it forms an increasingly larger reservoir (a to c).

pygidial glands. Thus, in several myrmicine species, in which we (Hölldobler et al 1976) and Kugler (1978) previously assumed the pygidial gland to be absent, we find that we now detect this organ by histological methods. Tables 1a and 1b list the species of the major subfamilies that we investigated histologically and indicate the type of tergal glands found.

b. Postpygidial gland

Dorsal glandular structures which open posteriorly to the pygidial gland, between the 7th and 8th abdominal terga (spiracular plate), we call postpygidial glands (Fig. 8). Whelden (1957, 1960) described glands in the 5th gastral segment of *Rhytidoponera convexa* and *R. metallica*. For *R. convexa* he writes: "Even the largest of these is less than half the size of the fourth-segment glands In the extreme case, there may be but a single gland cell on each side. It is often difficult to distinguish such a unicellular gland from an oenocyte, despite the usually distinct difference in size of the two cell types. Only the identification of a duct certainly distinguishes such a gland from the ductless oenocyte. In many individuals this second pair of glands could not be found". Whelden (1960) makes similar statements for *R. metallica*. Our results are somewhat different. We found well developed postpygidial glands in the 4 species of *Rhytidoponera* investigated (Table 1a). In all specimens we found a pair of clusters of glandular cells. Each cluster contains about 15-20 cells and each cell sends a duct through the intersegmental membrane close to the spiracular plate (Fig. 9, 10). In some ant species the postpygidial gland consists of only a few glandular cells, in others the postpygidial gland is associated with a well developed reservoir (Table 1a, 1b).

Sternal glands

In several species we discovered intersegmental sternal glands (Table 2). They can consist of a few glandular cells that send their channels through the intersegmental membrane, or of large clusters of glandular cells associated with voluminous reservoirs. These reservoirs are formed by invaginations of the intersegmental membranes (Fig. 8).

In several *Leptogenys* species (Fig. 12) we found two large sternal glands with reservoirs between the 7th and 6th, and 6th and 5th sterna. The latter glandular organ is usually associated with a special cuticular structure on the 6th sternum (Fig. 12). In *Paltothyreus*

tarsatus we found well developed sternal glands between the 7th and 6th, 6th and 5th, and 5th and 4th sterna, but no reservoirs. Instead, the duct openings are associated with filament-like protrusions of the intersegmental membrane (Fig. 13, 14).

Other abdominal glands

The glandular venom apparatus of ants is composed of the Dufour's gland (alkine or accessory gland) and the poison gland. Although the venom apparatus of ants is very well studied (see reviews by Maschwitz and Kloft 1971, Blum and Hermann 1978 a, b), other glands, such as Koschevnikov's gland (sting gland), Bördas's gland and sting sheath glands, known from other Hymenoptera, have not been firmly established in ants.

Koschevnikov (1899) found in honeybees and *Vespa* paired clusters of glandular cells located laterally near the intersegmental membrane between the quadrate plate and the spiracular plate. Each individual cell sends channels into gathering ducts, which connect with the intersegmental membrane. Altenkirch (1962) found similar glands in most Apidae that she had studied.

There are indications that this gland might also be present in some species of the primitive ant subfamilies Myrmeciinae and Ponerinae. Whelden (1957) described a pair of clusters of gland cells, located slightly dorsally on each side of the sting of *Stigmatomma* (= *Amblyopone*) *pallipes*. Each cell sends a "rather tortuous duct . . . down and inward, to open through a membrane which is above the sting". Robertson (1968) found "sting glands" in *Rhytidoponera* "toward the region of the triangular plate, where they are attached to the intersegmental membrane". She described similar glands in *Bothroponera* sp. (= *Pachycondyla*), *Leptogenys sjostedji* and *Myrmecia gulosa*. In the latter species the glands are described as "two well formed masses of gland cells, each cell attached to the intersegmental membrane in the region of the triangular plate by a long, simple, cuticular duct".

Table 3 (A) lists the species in which we found paired glandular structures, closely resembling the "sting glands" described by Robertson. In all cases the glandular cells are located near the triangular plate, and from each cell a rather long duct leads downwards and opens through a membrane near the base of the sting (Fig. 15). Although we could not precisely locate the openings of the ducts, we assume they opened in the sting chamber.

Altenkirch (1962) and Maschwitz (1964) discovered a so-called sting sheath gland in several bee species. It consists of a palisade epithelium located in the sheath valves. In some ant species we found a distinct palisade epithelium in the sheath valves and/or single glandular cells with long individual ducts (Table 3 (B), Fig. 16, 17). Janet (1898) describes similar single gland cells, located near the sheath valves, in *Myrmica rubra*.

Bordas's glands, as they were described by Bordas (1895) in Terebrantia and reexamined by Rathmayer (1962) in several sphecoid wasps, could not be identified in ants, although some of clusters of the single gland cells which send their ducts through the membrane of the sheath valves could be related to the Bordas's glands. It is obvious to us that the glandular structures, associated with the sting apparatus of ants, need to be investigated in greater detail in future studies.

In several ant species (Table 3 (C)) we found a highly developed palisade epithelium in the 7th sternum (Fig. 8). It is especially conspicuous in several *Leptogenys* species and in the army ants *Eciton* and *Neivamyrmex*, but it is not strongly developed in *Dorylus*. In the dolichoderine species and in *Aneuretus* this epithelium seems to be closely associated with the sternal gland (Pavan's gland).

In the African weaver ant (*Oecophylla longinoda*) we discovered a sternal gland under the 7th sternum, which is quite different from the glandular epithelium described above (Hölldobler and Wilson 1976, 1978). This structure consists of an array of single glandular cells that send short channels into cuticular cups on the outer surface of the sternite. In none of the other formicine species investigated, listed in table 1b, did we find this type of sternal gland. But in *Camponotus sericeus* we detected different clusters of glandular cells in the last sternum. Each cell sends a long channel through the intersegmental membrane near the vagina into the ventral part of the "sting chamber". We discovered similar paired glandular cell clusters in most myrmicine species we investigated. The gland is especially distinct in *Novomessor* and *Veromessor*, where the glandular cell channels penetrate the membrane near the vagina (Fig. 18).

The function of the intersegmental glands:

The functions of most of the glandular structures described in this paper are not yet known, but in a few species the function of the

pygidial gland has already been identified. In *Novomessor cockerelli* and *N. albisetosus* the strongly smelling secretion of the pygidial glands releases a "panic alarm" response in workers, apparently specifically designed against army ant predation (Hölldobler in prep.). Kugler (in press) demonstrated that in *Pheidole biconstricta* the pygidial glands produce an alarm-defense secretion. A quite different function has been discovered in *Rhytidoponera metallica*. Here the wingless virgin females attract males by the release of a pheromone from the pygidial gland (Hölldobler and Haskins 1977). Since *Rhytidoponera* workers also have a well-developed pygidial gland and are attracted to its secretions, we believe we have not yet discovered the whole functional spectrum of this organ. In *Leptogenys chinensis*, Maschwitz and Schönege (1977) demonstrated that the pygidial gland secretions serve together with poison gland substances as a recruitment trail pheromone. We obtained similar results when we recently reexamined the anatomical source of the trail pheromone of *Pachycondyla* (= *Termitopone*) *laevigata*. This ant species conducts well organized predatory raids on termites. During raiding the workers move in a single file, one closely behind another, along a powerful trail pheromone laid down by leading scout ants. Blum (1966) has identified the hindgut as the source of this recruitment trail pheromone. We cannot confirm his findings.

In our experiments with artificial trails laid with extracts from several abdominal glands, only the pygidial gland secretions released massive trail-following behavior in *P. laevigata* (Hölldobler and Traniello in prep.). A careful observational study of the trail-laying behavior of *P. laevigata* workers revealed that not the anus but rather the pygidial gland is dragged over the ground. Although the pygidial gland of *P. laevigata* has no definite reservoir, it is very well developed and is associated with an elaborate cuticular structure on the 7th tergum (Fig. 19, 20). The glandular secretion is apparently stored in the many cavities of this structure. When trailing, the ants rub this structure with its special applicator surface over the ground and deposit thereby the trail pheromone. Traniello (pers. communication) observed species of *Odontomachus* during nest emigrations performing the same trail laying behavior. We suspect that in *Odontomachus* also the pygidial gland secretes a trail pheromone (Fig. 21).

In *Bothroponera* (= *Pachycondyla*) *tesserinoda* we previously analyzed the signals involved in the tandem running recruitment technique (Hölldobler et al 1973, Maschwitz et al 1974). We

discovered that the cues responsible for "binding" the follower behind the leader ant include both a surface pheromone and mechanical stimuli. Although we could extract this surface pheromone, we were not able to identify its anatomical source; all experiments with secretions from the known exocrine glands had negative results. After the recent discovery of the pygidial gland in *Pachycondyla* we have begun to conduct tandem running experiments with *Pachycondyla crassa** and *P. harpax**, using dummies contaminated with pygidial gland secretions. Our preliminary results strongly indicate that pygidial gland substance might be the source of the tandem running pheromone in these species.

In the doryline army ants raiding and emigrations are conducted along chemical trails deposited by workers. For *Neivamyrmex*, Watkins (1964) and Watkins et al (1967), and for *Eciton hamatum*, Blum and Portocarrero (1964), identified the hindgut as the source of the trail pheromone. In addition, Chadab and Rettenmeyer (1975) and Topoff and Mirenda (1975) demonstrated that besides the relatively long-lasting hindgut trail-substance, other signals (possibly more volatile secretions) are involved in the organization of "mass recruitment" in *Eciton* and *Neivamyrmex*.

We believe that our morphological investigations provide new possibilities for the analysis of chemical communication in army ants. Both *Neivamyrmex* and *Eciton* have large pygidial glands with distinct reservoirs (Fig. 22, 23). The postpygidial gland is smaller, but still considerably larger than in most of the other investigated species†. In both army ant species the 7th tergum is relatively small. Therefore, the reservoirs of the pygidial gland and postpygidial gland open directly above the anus at the abdominal tip (Fig. 23). In workers (all castes) of *Eciton* the dorsal membrane near the exits of the reservoir of the pygidial glands is conspicuously modified to a brush-like structure (Fig. 24). These morphological features strongly

* *P. crassa* was observed tandem running by W. L. Brown, Jr. (pers. communication) at the western base of Ubombo Mts., Zululand, and by B. Hölldobler in Shimba Hills Reserve (Kenya). *P. harpax* was observed tandem running by S. Levings (pers. communication) on Barro Colorado Island, Panama.

† Whelden (1963) described two glands at the extreme posterior end of the gaster of *Eciton burchelli* workers. Although the description is not very accurate, from his drawings we can conclude that he found the pygidial gland and postpygidial glands.

suggest that the tergal glands might be involved in the chemical trail communication of army ants. We have begun to test this hypothesis with *Eciton hamatum*. The pygidial gland secretion of *E. hamatum* has a strong, characteristic smell. The secretion is probably skatole (Traniello pers. communication), the substance that gives army ants their typical "fecal odor". Recently Brown et al (1978) demonstrated that skatole is an effective growth inhibitor for bacteria and fungi and repels insectivorous snakes (Watkins et al 1969). Our first, preliminary tests demonstrated that *Eciton* workers follow artificial trails drawn with crushed pygidial glands. When we simultaneously offered trails drawn with hindgut contents and pygidial gland secretions, the latter were significantly preferred during the first minute. When we used trails drawn with secretions of the poison gland or Dufour's gland as controls, the ants always followed the pygidial gland trails. We have to stress, however, that these experiments must be considered pilot tests. The preliminary results, however, are striking enough to warrant a more detailed investigation in the future. It is interesting to note that the anatomy of the pygidial gland in the African army ant, *Dorylus molesta*, is quite different from that of *Eciton* and *Neivamyrmex* (Fig. 25). In this species the 7th tergum is considerably larger than in species of the latter genera, and the reservoirs of the pygidial glands do not open at the abdominal tip. In *Dorylus*, however, we found single glandular cells with channels opening directly at the anus, a feature we have not detected in other ant species (Fig. 25, 26).

Finally, our morphological study of the pygidial gland of *Veromessor pergandei* has led to results that are suggestive of the function of this organ. In this species the 7th tergum is relatively small, and as a result the large reservoirs of the pygidial glands open at the tip of the gaster (Fig. 27). *Veromessor* forages in well-organized columns (Went et al 1972; Wheeler and Rissing 1975; Bernstein 1975). Several observations suggest that these foraging columns are organized by a trail pheromone, though no trail pheromone gland has yet been identified. Clearly, the large pygidial gland has to be considered as a possible source for the trail pheromone.

The function of most of the newly discovered sternal glands is unknown. Only in *Paltothyreus tarsatus* could we demonstrate experimentally that foragers lay a recruitment trail with sternal gland secretions (Hölldobler in prep.).

CONCLUSIONS

Since we first found the pygidial gland widespread in the subfamilies Myrmeciinae and Ponerinae, we speculated that this gland might be a primitive monophylogenetic trait in ants generally (Hölldobler and Haskins 1977). The results reported in the present paper fully confirm this assumption. A well-developed pygidial gland was found in the most primitive ant, *Nothomyrmecia macrops*, and in representatives of all major subfamilies except in the Formicinae (Table 1b). We agree with Kugler (1978) that the "anal glands" of the Dolichoderinae and Aneuretinae are homologous to the pygidial glands of other ant subfamilies. Considering the variation in the morphology of the pygidial glands, even within a single subfamily, we think that the morphological variation of the "anal glands" of dolichoderine and aneuretine species does not warrant a separate terminology. In fact the term "anal gland" is misleading, because the glands do not exit from the anal opening of the gaster, as is sometimes inferred, but between the 6th and 7th abdominal terga (Fig. 28). This was clearly demonstrated by Pavan and Ronchetti (1955). It is our view and also Kugler's (pers. communication) that the "anal glands" should be called pygidial glands.

Kugler (1978) concluded from his comparative studies of myrmicine species that usually those species that have reduced or modified stings also have well-developed pygidial glands. He assumes that the pygidial gland replaces the sting apparatus as a chemical defense device. Our finding that well-developed pygidial glands occur in *Pogonomyrmex*, a genus with a very effective sting apparatus, and in many stinging ponerine species, does not support Kugler's conclusions.

ACKNOWLEDGEMENTS

This paper would not have been possible without the help of many people. We would like to thank all the collectors mentioned in Table 1, including Donald W. Windsor, who helped finding the acacias in the Canal Zone. Special thanks to Robert W. Taylor, who sent us the precious *Nothomyrmecia*. Barry Bolton, William L. Brown, Jr., William H. Gotwald, Jr. and Roy Snelling identified many species for us. We are grateful to Ed Seling for his superb assistance during the SEM work. Frank M. Carpenter's many suggestions improved the manuscript greatly. This work was supported by NSF grant BNS 77-03884.

TABLE Ia

List of species of the poneroid complex (Taylor 1978) that were investigated histologically, and the types of tergal glands found. When the histological series was incomplete and we could not make a definite statement, the column is marked with "?". When the cuticular structure on the pygidium was only slightly sculptured, we marked the column with "-(+)".

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
MYRMECINAE						
<i>Myrmecia pilosula</i>	R. J. Bartell R. W. Taylor Brindabella Ranges, Australia	+		-	-	+
PONERINAE						
<i>Amblyopone australis</i>	C. P. Haskins Manjimup, W. Australia	+		-	-	-
<i>Amblyopone pallipes</i>	J. Traniello Carlisle, Mass.	+		-	-	-
<i>Platythyrea cribinoda</i>	K. Horton R. Silberglied Shimba Hills, Kenya	+		-		+
<i>Rhytidoponera metallica</i>	C. P. Haskins Blackwell Range, Queensland, Australia	+		-		+
<i>Rhytidoponera perthensis</i>	C. P. Haskins Boddington, W. Australia	+		-		+
<i>Rhytidoponera purpurea</i>	C. P. Haskins Black Mountain, Kuranja, Queensland	+		-		+

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
<i>Rhytidoponera violacea</i>	C. P. Haskins Kings Park, W. Australia	+		-		+
<i>Paltothyreus tarsatus</i>	B. Hölldobler Shimba Hills, Kenya		+	-		+
<i>Pachycondyla crassa</i>	B. Hölldobler Shimba Hills, Kenya	+		-		+
<i>Pachycondyla laevigata</i> (= <i>Termitopone</i>)	N. Franks J. Traniello BCI, Panama		+	+	?	?
<i>Plectroctena strigosa</i>	B. Hölldobler Shimba Hills, Kenya	+		+	+	
<i>Leptogenys neutralis</i>	C. P. Haskins Manjimup, W. Australia	+		+		+
<i>Leptogenys pavesii</i>	B. Hölldobler Shimba Hills, Kenya	+		+		+
<i>Leptogenys nitidia</i>	B. Hölldobler Shimba Hills, Kenya	+		+		+
<i>Leptogenys regis</i>	B. Hölldobler Shimba Hills, Kenya	+		+		+
<i>Odontomachus haematoda</i>	C. P. Haskins BCI, Panama	+		+		+

TABLE 1a Continued

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
DORYLINAЕ						
<i>Neivamyrmex nigrescens</i>	B. Hölldobler Arizona	+		-	+	
<i>Eciton hamatum</i>	A. Aiello R. Silberglied J. Traniello BCI, Panama	+		-	+	
<i>Dorylus molestus</i>	B. Hölldobler Shimba Hills, Kenya		+	+		+
PSEUDOMYRMECINAE						
<i>Pseudomyrmex ferruginea</i>	A. Aiello R. Silberglied Canal Zone, Panama	+		-		+
<i>Pseudomyrmex pallidus</i>	M. Möglich Florida	+		-		?
<i>Tetraponera spec. (78/26)</i>	B. Hölldobler Shimba Hills, Kenya	+				+
MYRMECINAE						
<i>Myrmica americana</i>	J. Traniello Carlisle, Mass.		+	-	-	-
<i>Tetramorium caespitum</i>	J. Traniello Carlisle, Mass.		+	-	-	-
<i>Pogonomyrmex desertorum</i>	B. Hölldobler Arizona		+	-(+)	-	-
<i>Pogonomyrmex californicus</i>	B. Hölldobler Arizona		+	-(+)	-	-

TABLE 1a Continued

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
<i>Pogonomyrmex badius</i>	B. Hölldobler Florida		+	-	-	-
<i>Veromessor pergandei</i>	G. Alpert Mexico	+		-	-	-
<i>Novomessor cockerelli</i>	B. Hölldobler Arizona		+	+	-	-
<i>Novomessor albisetosus</i>	B. Hölldobler Arizona		+	+	-	-
<i>Aphaenogaster rudis</i>	J. Traniello Concord, Mass.		+	-	-	-
<i>Aphaenogaster huachucana</i>	B. Hölldobler Arizona		+	-	-	-
<i>Pheidole militicida</i> (worker & soldier)	B. Hölldobler Arizona		+	-(+)	-	-
<i>Pheidole desertorum</i>	B. Hölldobler Arizona	+		+	-	-
<i>Atta sexdens</i> (several castes)	N. Weber Timehri, Guyana	-	-	-	-	-

TABLE 1a Concluded

TABLE 1b

List of species of the formicoid complex (Taylor 1978) that we investigated histologically, and the types of tergal glands found.

Subfamily/Species	Collector and Locality	Pygidial gland with definite reservoir	Pygidial gland without definite reservoir	Pygidial gland with special cuticular structure on pygidium	Postpygidial gland with reservoir	Postpygidial gland without reservoir
NOTHOMYRMECINAE						
<i>Nothomyrmecia macrops</i>	R. W. Taylor Eyre Peninsula S. Australia	+		-		+
ANEURETINAE						
<i>Aneuretus simoni</i>	E. O. Wilson Ratnapura, Sri Lanka	+		-	-	-
DOLICHODERINAE						
<i>Liometopum apiculatum</i>	B. Hölldobler Arizona	+		-	-	-
<i>Conomyrma bicolor</i>	B. Hölldobler Arizona	+		-	-	-
<i>Iridomyrmex pruinosus</i>	B. Hölldobler Arizona	+		-	-	-
FORMICINAE						
<i>Oecopylla longinoda</i>	B. Hölldobler Shimba Hills, Kenya	-	-	-	-	-
<i>Pachycondyla</i> spec.	R. Silberglied Nairobi Arboretum, Kenya	-	-	-	-	-
<i>Myrmecocystus mexicanus</i>	B. Hölldobler Arizona	-	-	-	-	-
<i>Myrmecocystus mimicus</i>	"	-	-	-	-	-
<i>Myrmecocystus mendax</i>	"	-	-	-	-	-
<i>Formica perpilosa</i>	"	-	-	-	-	-
<i>Camponotus sericeus</i>	M. Mögliche Sri Lanka	-	-	-	-	-

TABLE 2

List of species of the poneroid complex in which we found intersegmental sternal glands.

Species	Location of glands between abdominal segments					
	7 and 6		6 and 5		5 and 4	
	reservoir		reservoir		reservoir	
	yes	no	yes	no	yes	no
<i>Myrmecia pilosula</i>		+				
<i>Rhytidoponera purpurea</i>		+				
<i>Paltothyrcus tarsatus</i>		+		+		+
<i>Pachycondyla crassa</i>		+		+		?
<i>Leptogenys neutralis</i>	+		+			
<i>Leptogenys pavesii</i>	+		+			
<i>Leptogenys nitida</i>	+		+			
<i>Leptogenys regis</i>	+		+			
<i>Tetraponera</i> sp. (78/26)		+		+		+

TABLE 3

List of species, where sting glands (A), sting sheath glands (B), and a glandular epithelium in the 7th sternum (C) were found. In species marked with "(?)" the histological series was not complete and we could therefore not trace the whole glandular structure. Species which have only a glandular epithelium in the sting sheath are marked with (+); those with glandular epithelium and single gland cells with ducts are marked with (++); in unmarked species only single glandular cells with ducts were found.

A	B	C
<i>Myrmecia pilosula</i>	<i>Nothomyrmecia macrops</i>	<i>Leptogenys neutralis</i>
<i>Amblyopone australis</i>	<i>Myrmecia pilosula</i>	<i>Leptogenys pavesii</i>
<i>Amblyopone pallipes</i>	<i>Amblyopone australis</i>	<i>Leptogenys nitida</i>
<i>Rhytidoponera metallica</i>	<i>Amblyopone pallipes</i>	<i>Leptogenys regis</i>
<i>Rhytidoponera perthensis</i>	<i>Rhytidoponera purpurea</i>	<i>Eciton hamatum</i>
<i>Rhytidoponera purpurea</i>	<i>Platythyrea cribinoda</i>	<i>Neivamyrmex nigrescens</i>
<i>Rhytidoponera violacea</i>	<i>Paltothyreus tarsatus</i>	<i>Aneuretus simoni</i>
<i>Platythyrea cribinoda</i>	<i>Leptogenys nitida</i>	<i>Iridomyrmex pruinosus</i>
<i>Paltothyreus tarsatus</i>	<i>Leptogenys regis</i>	<i>Conomyrma bicolor</i>
<i>Leptogenys regis</i>	<i>Odontomachus haematoda</i>	<i>Liometopum apiculatum</i>
	<i>Myrmica americana</i>	<i>Novomessor cockerelli</i>
		<i>Novomessor albisetosus</i>

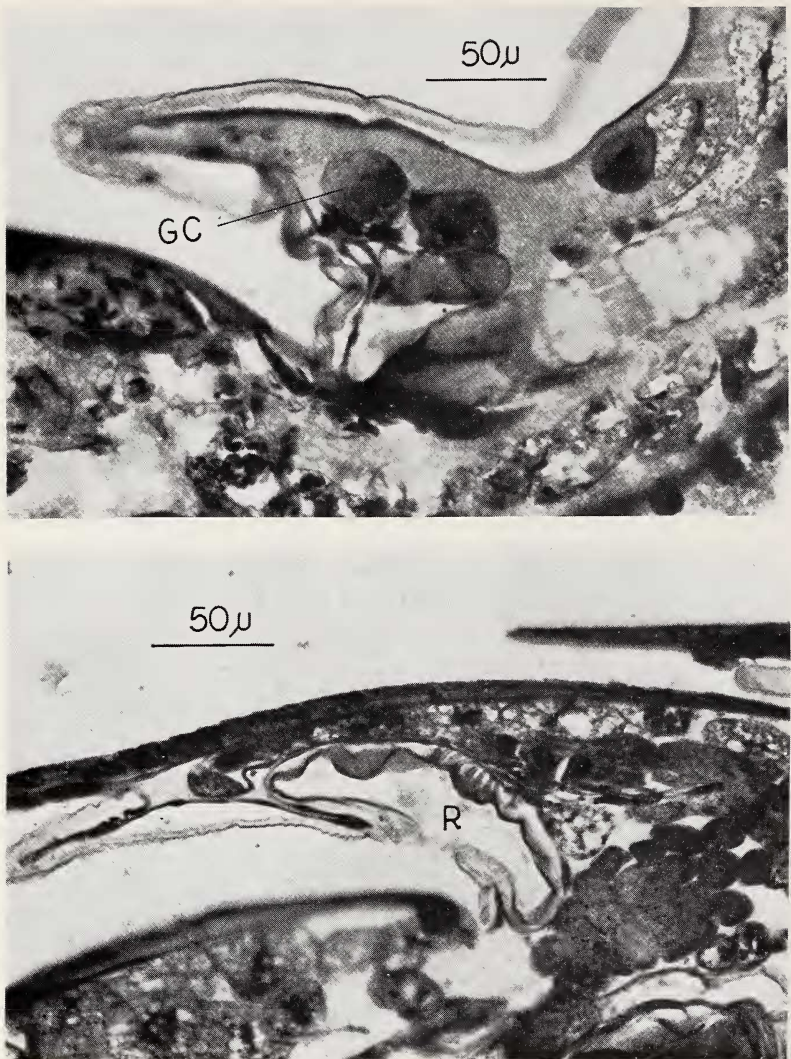


Figure 2. Above: Sagittal section through pygidial glands of *Amblyopone australis*. The gland has no distinct reservoir, but 10-15 glandular cells (GC) with channels in each cluster. Below: Pygidial gland of *Amblyopone pallipes* with distinct reservoir (R) and 30-40 glandular cells in each cluster.

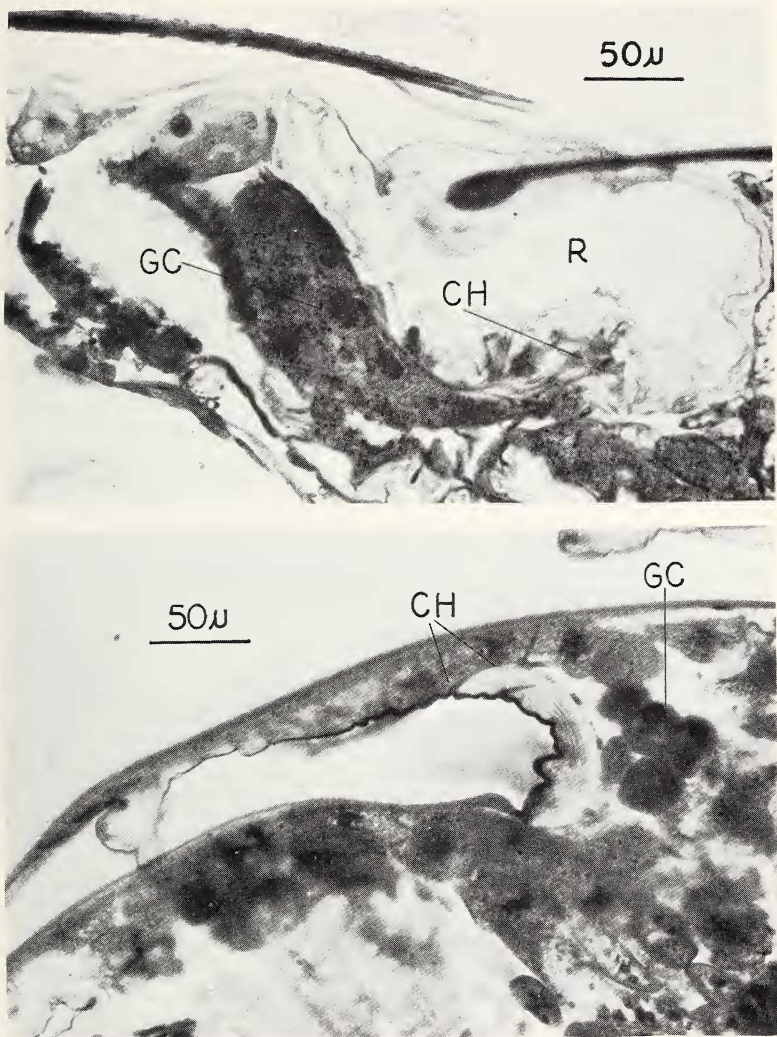


Figure 3. Above: Sagittal section through pygidial glands of *Nothomyrmecia macrops*: Very large reservoir (R); each cluster consists of 50–80 cells; GC = glandular cells; CH = channels of glandular cells. Below: Pygidial gland of *Myrmica americana*: No distinct reservoir, 10–15 cells in each cluster.

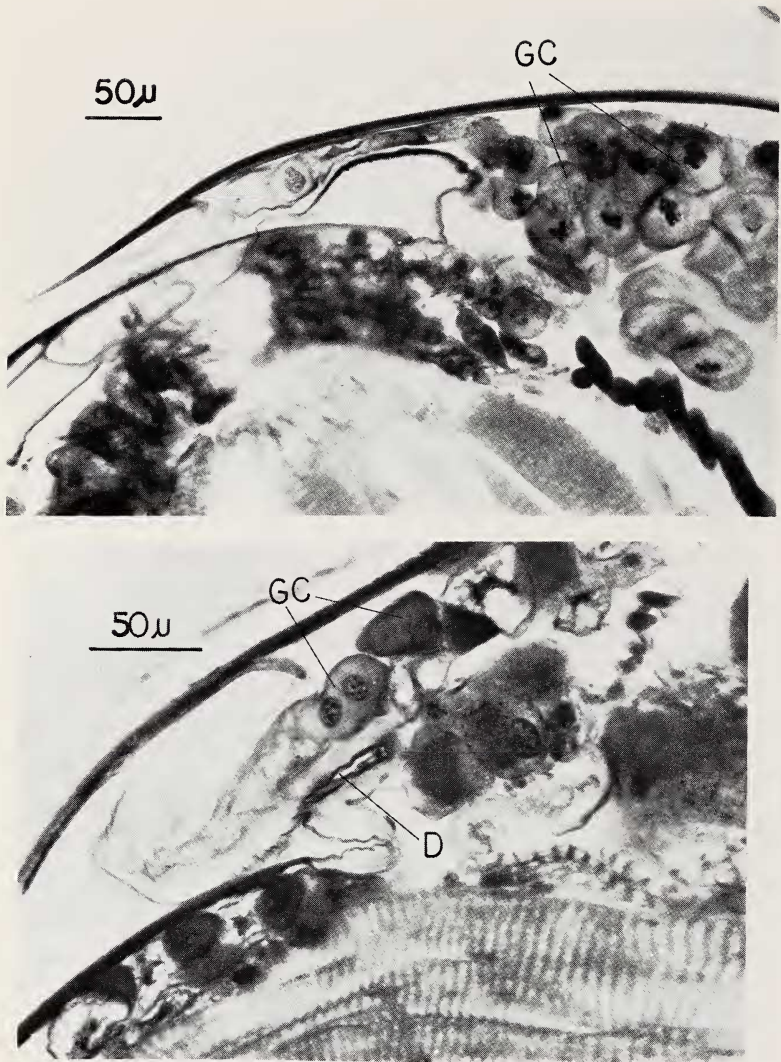


Figure 4. Above: Sagittal section through pygidial glands of *Pogonomyrax californicus*: No definite reservoir, but large cell clusters, each containing 30–35 glandular cells (GC). Below: Pygidial gland of *Pseudomyrmex ferruginea*: No distinct reservoir; intersegmental membrane forms a chitinous duct (D) into which the individual glandular channels open.

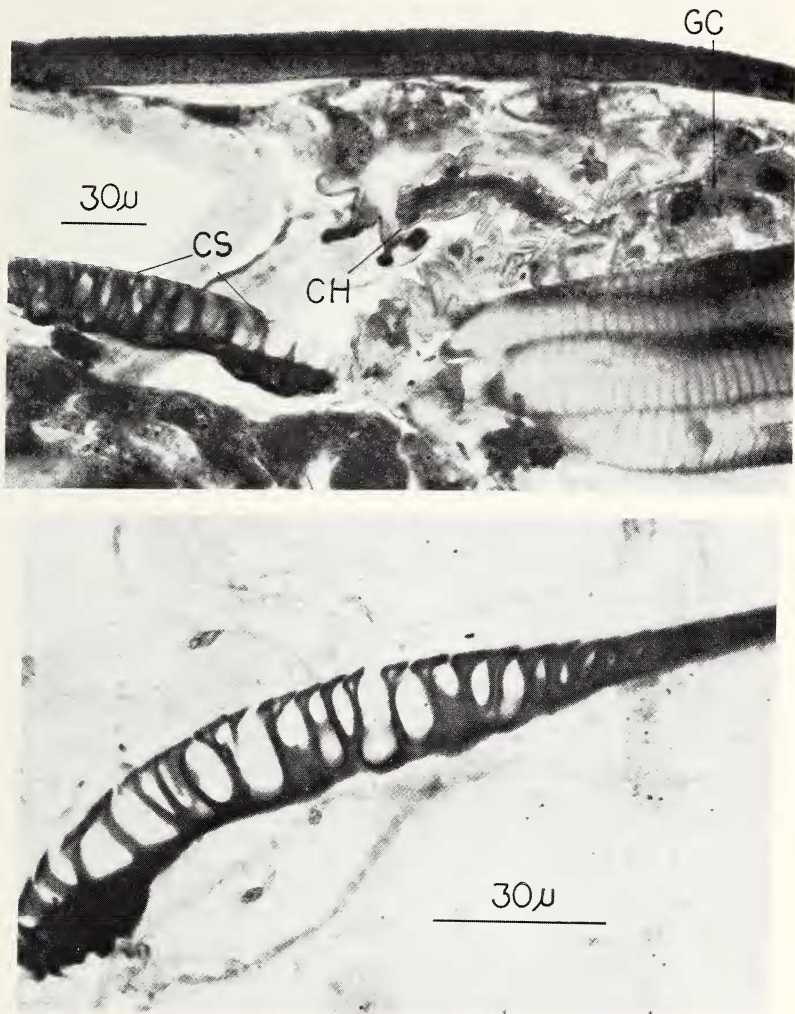


Figure 5. Above: Sagittal section through the pygidial gland of *Leptogenys pavesii* (GC = glandular cells; CH = channels of GC; CS = cuticular structure on the 7th tergum). Below: Close-up view of sagittal section through cuticular structure of 7th tergum of *Leptogenys neutralis*.

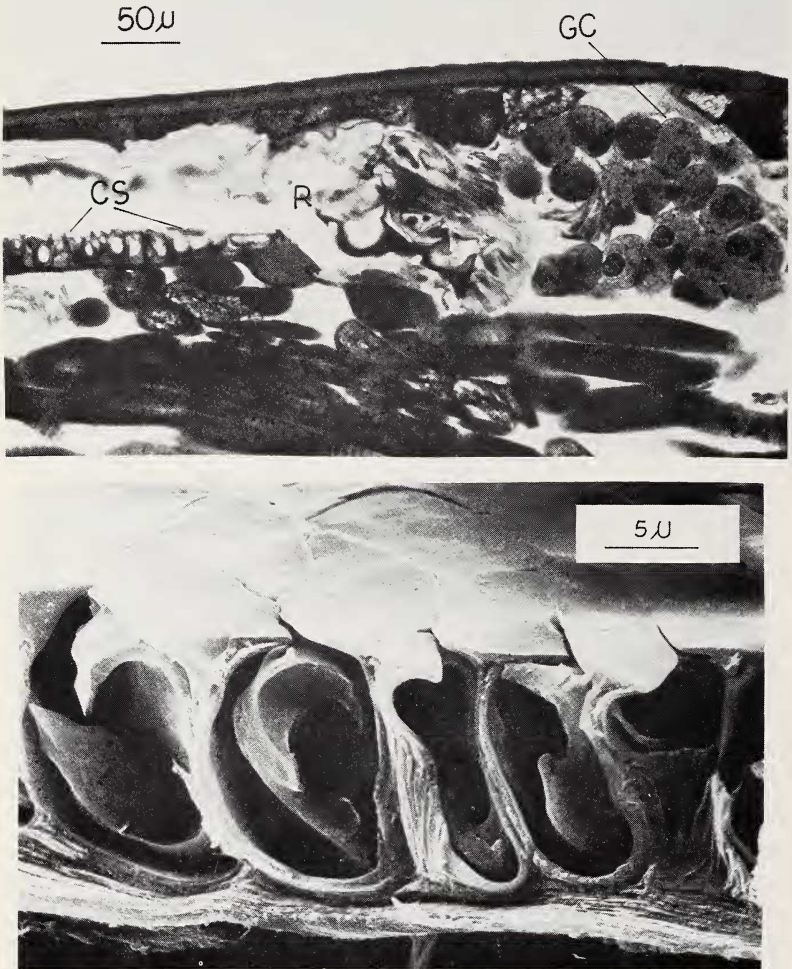


Figure 6. Above: Sagittal section through pygidial gland of *Leptogenys regis*. Below: SEM photograph of cuticular structure of 7th tergum of *L. regis*. The tergum is cut so that the well-structured cavities under the surface can be seen. (Lettering as in Fig. 5).

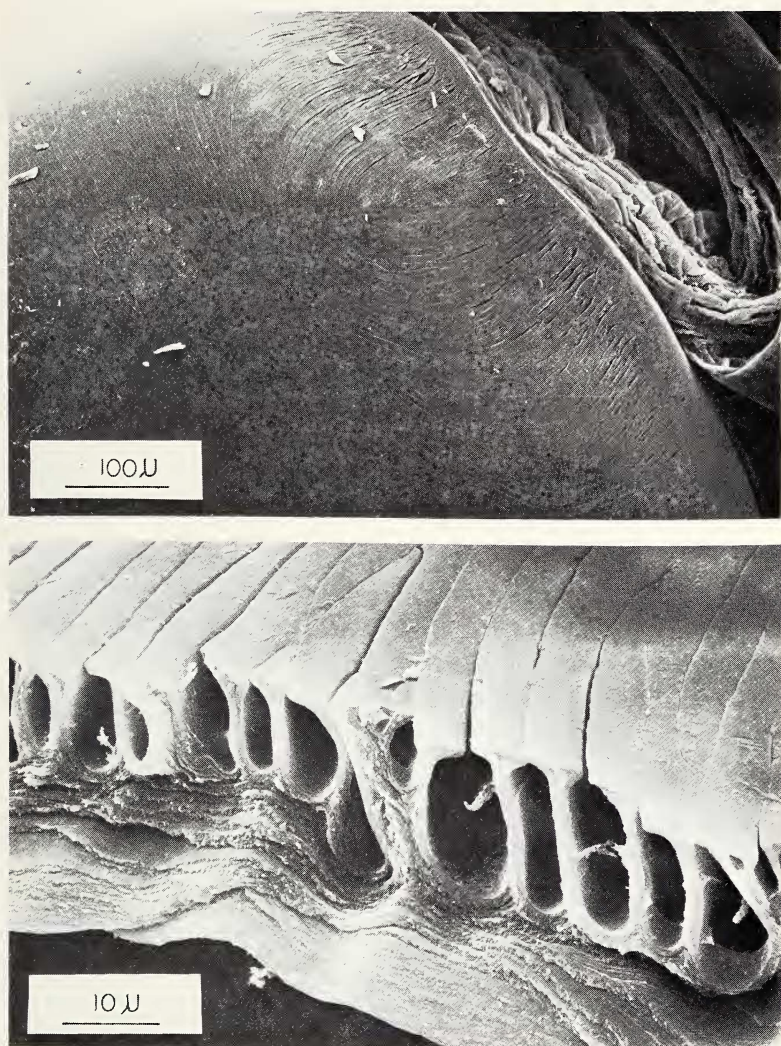


Figure 7. SEM photograph of cuticular structure of 7th tergum of *Plectroctena strigosa*. Above: View of the anterior part of the tergum. The cuticular grooves are clearly visible. Below: Close-up view of cuticular structure; the tergum is cut, so that the cavities beneath the grooves are visible.

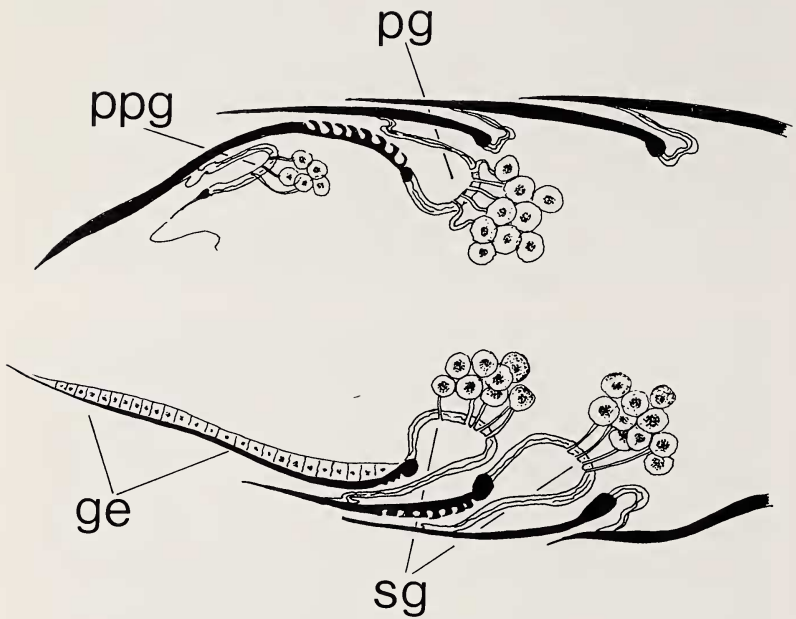


Figure 8. Schematic illustration of tergal and sternal glands in *Leptogenys*. (Lettering as in Fig. 5; sg = sternal gland; ge = glandular epithelium; ppg = post-pygidial gland; pg = pygidial gland).

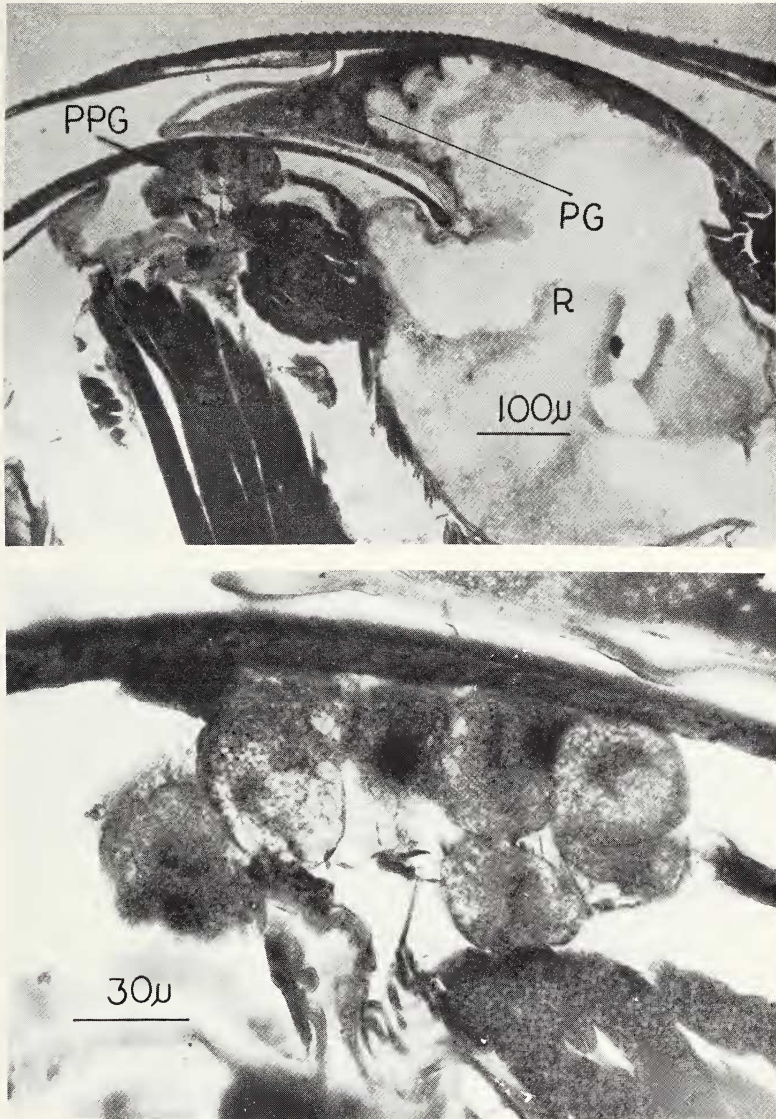


Figure 9. Above: Sagittal section through pygidial gland and postpygidial gland, with large reservoirs of *Rhytidoponera perthensis*. Below: Postpygidial gland only; note the glandular cells with channels. (Lettering as in Fig. 8; R = reservoir).

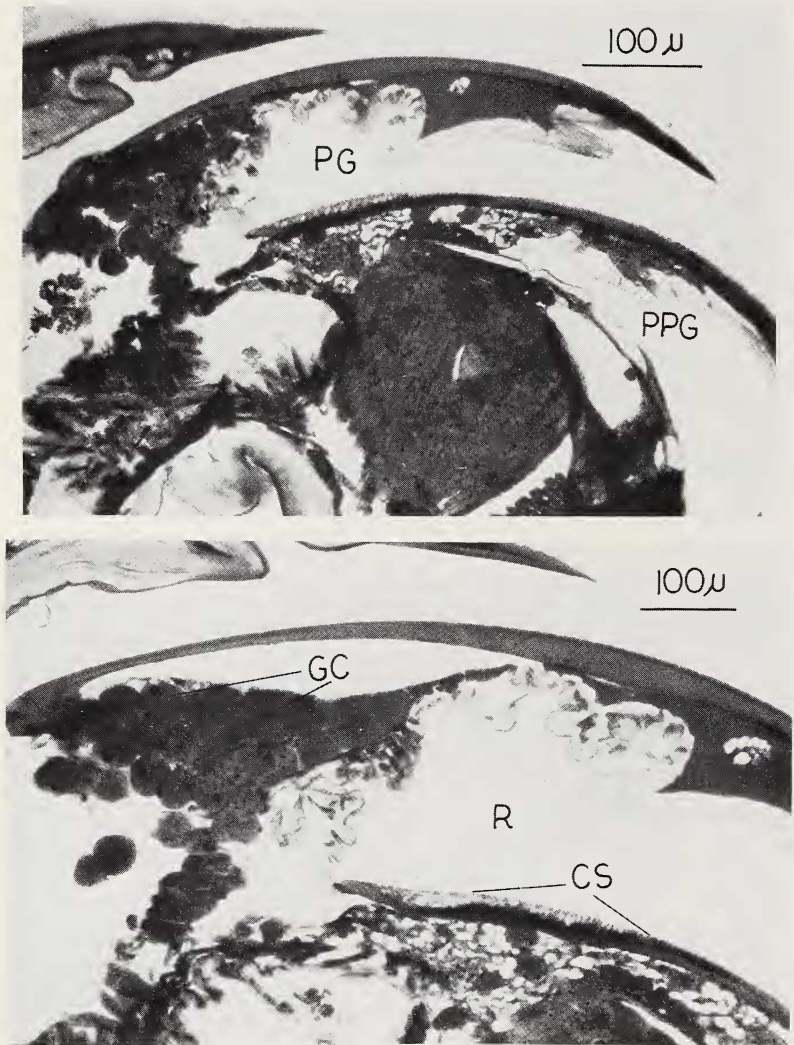


Figure 10. Above: Sagittal section through pygidial gland and postpygidial gland of *Plectroctena strigosa*. Below: Pygidial gland. (Lettering as in Fig. 5; PPG = postpygidial gland; PG = pygidial gland; R = reservoir).

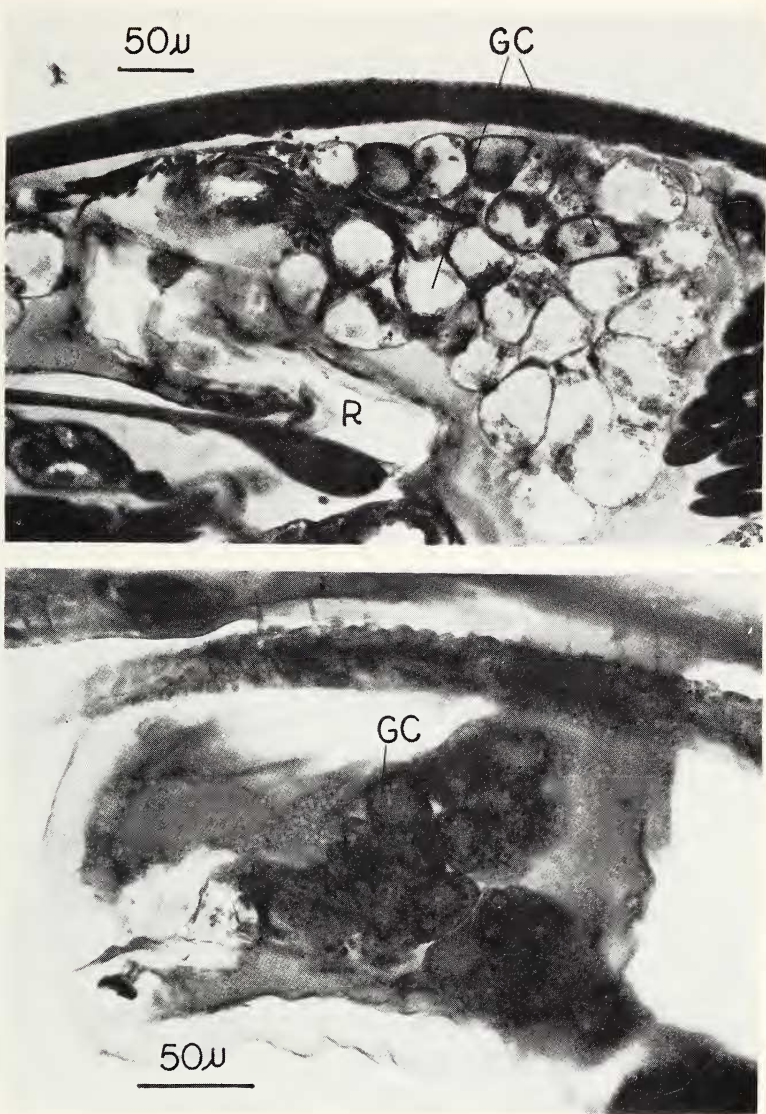


Figure 11. Above: Sagittal section through the pygidial gland of *Platythyrea cribinoda*. The large reservoir is folded in this section. Each cell cluster contains 50–70 cells. Below: Section through postpygidial gland of *P. cribinoda*; each cluster contains 15–20 cells. (Lettering as in Fig. 3).

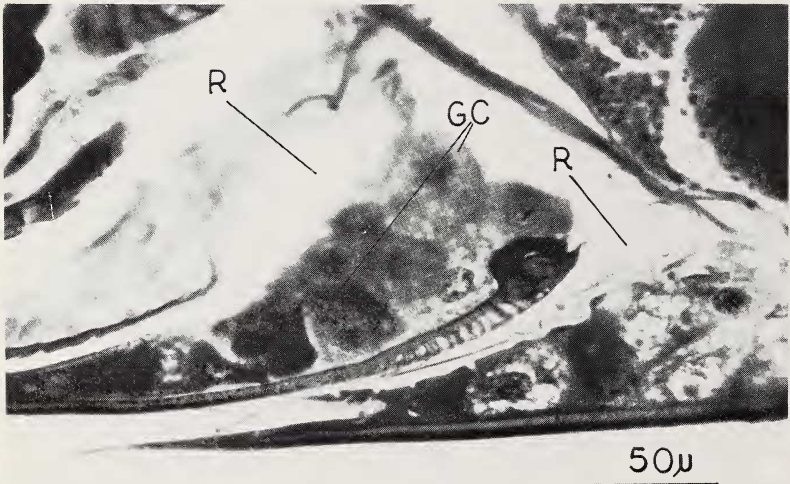
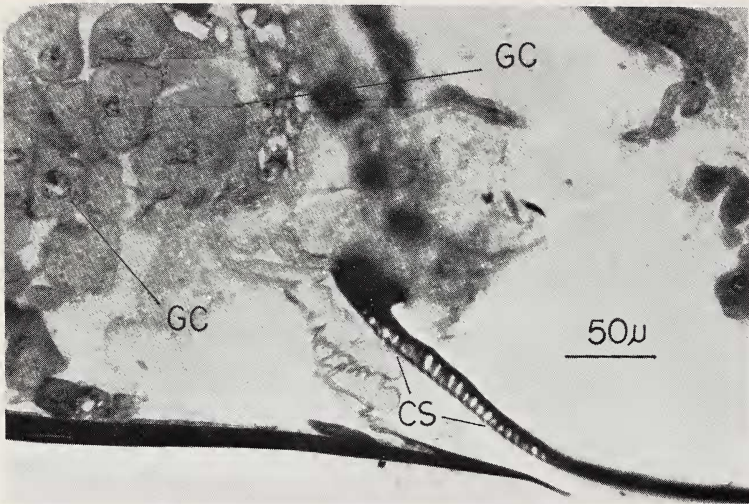


Figure 12. Above: Sagittal section through sternal gland between 5th and 6th sterna of *Leptogenys neutralis*. Usually the 6th sternum has a distinct cuticular structure (CS), very similar to that on the 7th tergum. Below: Section through both sternal glands (Between 5th and 6th, and 6th and 7th sterna) of *Leptogenys nitida*. (Lettering as in Fig. 5; R = reservoir).

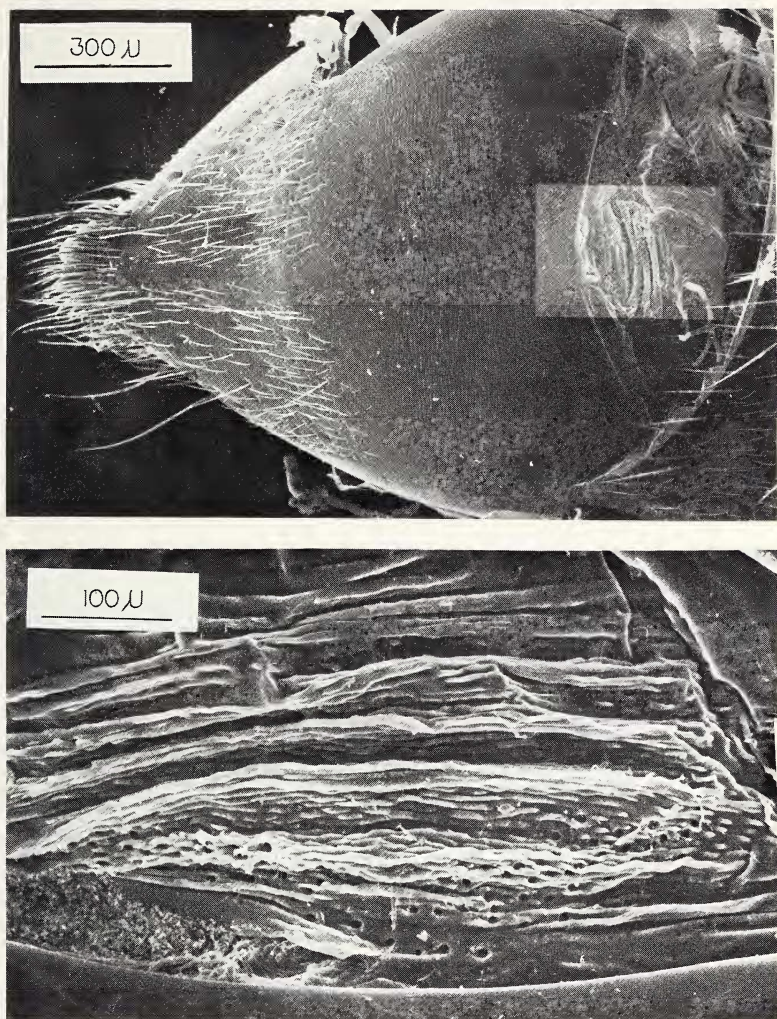


Figure 13. SEM photograph of the sternal gland area between the 6th and 7th sterna of *Paltothyreus tarsatus*. The picture below is an enlargement of the lighter rectangle in the picture above. The openings of the glandular cell channels in the intersegmental membrane are clearly visible.

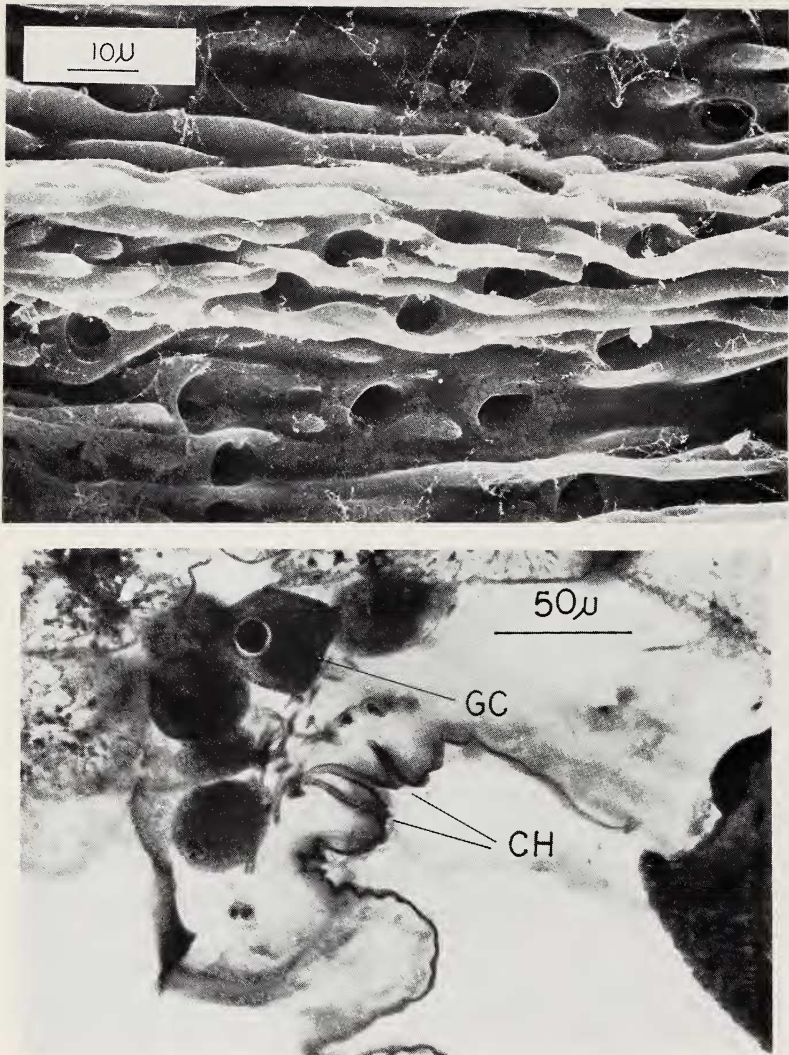


Figure 14. Above: SEM photograph of the glandular cell openings of the sternal gland of *Paltothyreus tarsatus*. Note the filament-like protrusions of the intersegmental membrane. Below: Sagittal section through the same area. (Lettering as in Fig. 5).

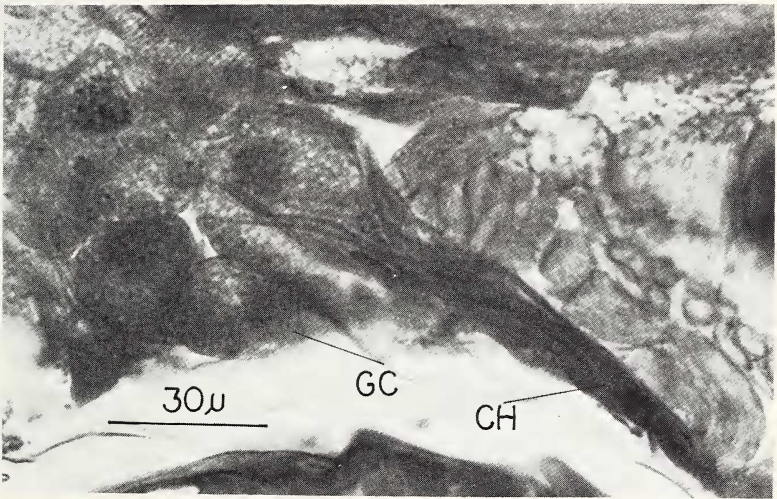
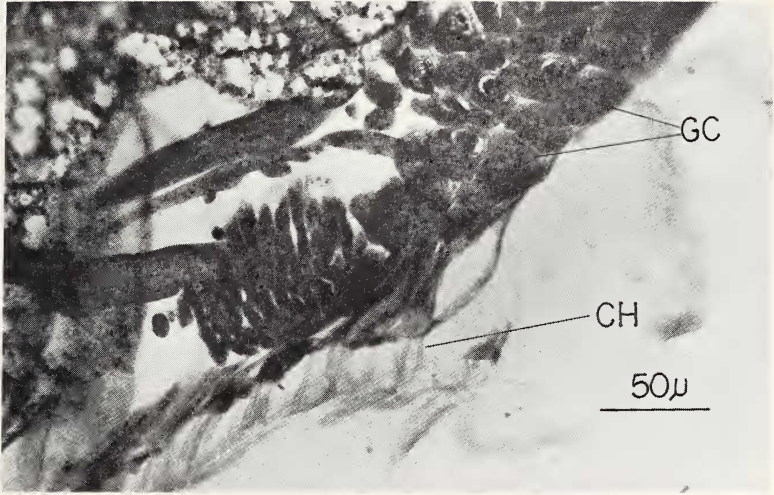


Figure 15. "Sting glands" of *Myrmecia pilosula* (above) and *Amblyopone pallipes* (below). (Lettering as in Fig. 5).

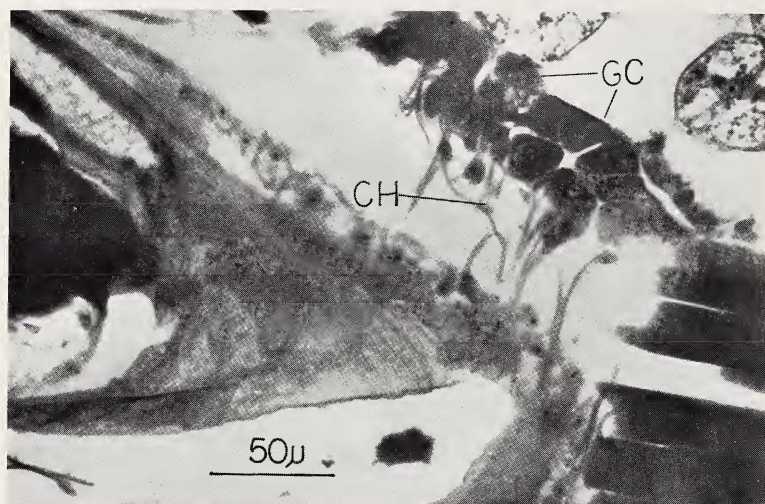
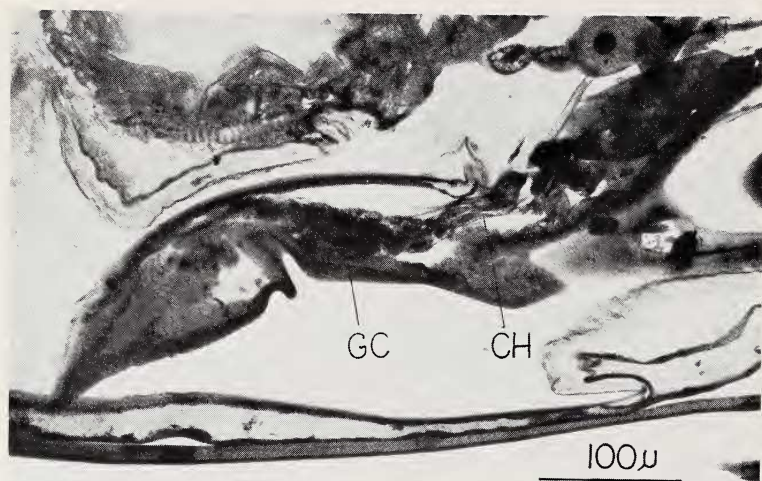


Figure 16. Glands associated with the sting sheath. Above: Sagittal section through sheath valve with glandular cluster and channels in *Odontomachus haematoda*. Below: *Myrmecia pilosula*. (Lettering as in Fig. 5).

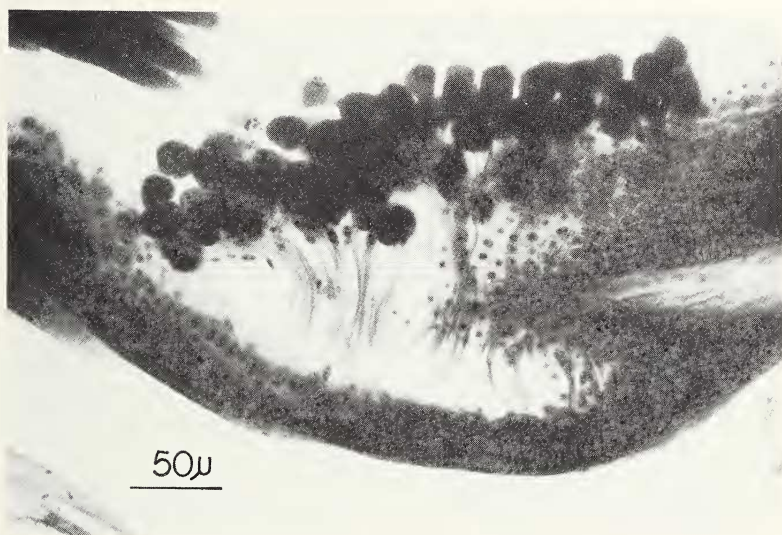
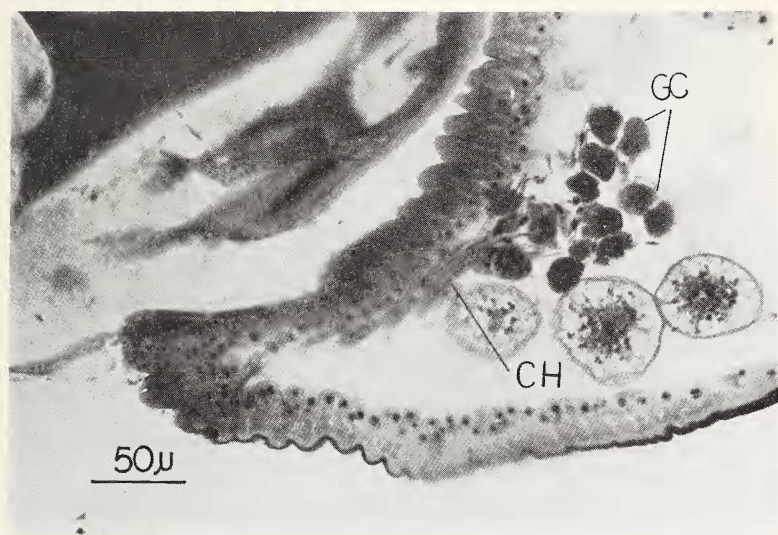


Figure 17. Glands associated with sting sheath in *Paltothryeus tarsatus*. Above: Sagittal section through glandular cells with channels. Below: Sagittal section through glandular cell cluster with channels. (Lettering as in Fig. 5).

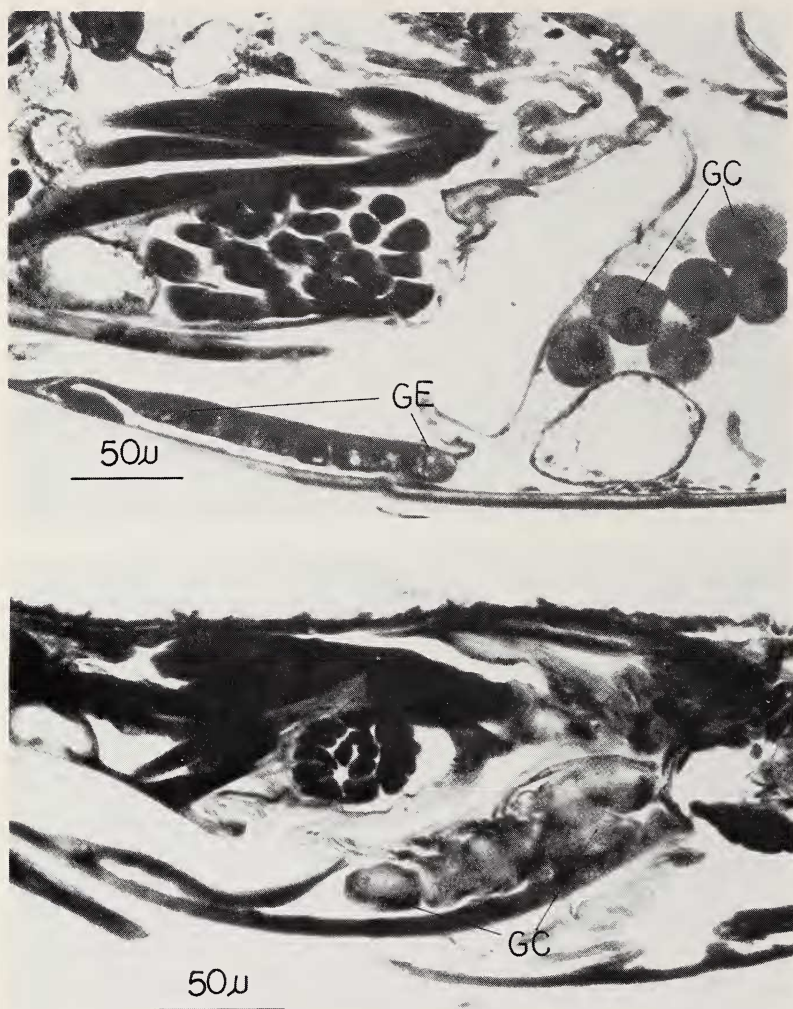


Figure 18. Glandular cell clusters in the 7th abdominal sternum of *Novomessor cockerelli* (above) and *Veromessor pergandei* (below). GE = glandular epithelium in the 7th sternum. (Lettering as in Fig. 5).

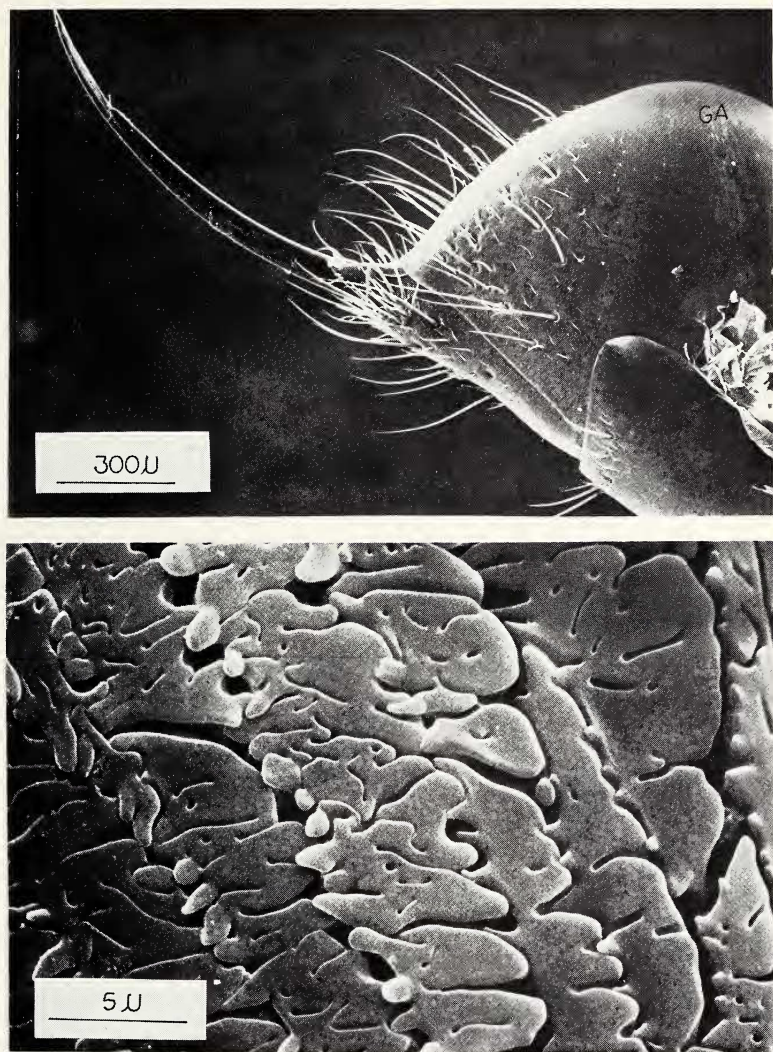


Figure 19. SEM photograph of the 7th tergum of *Pachycondyla* (= *Termitopone*) *laevigata*. Glandular applicator surface (GA) is shown in greater detail in the picture below.

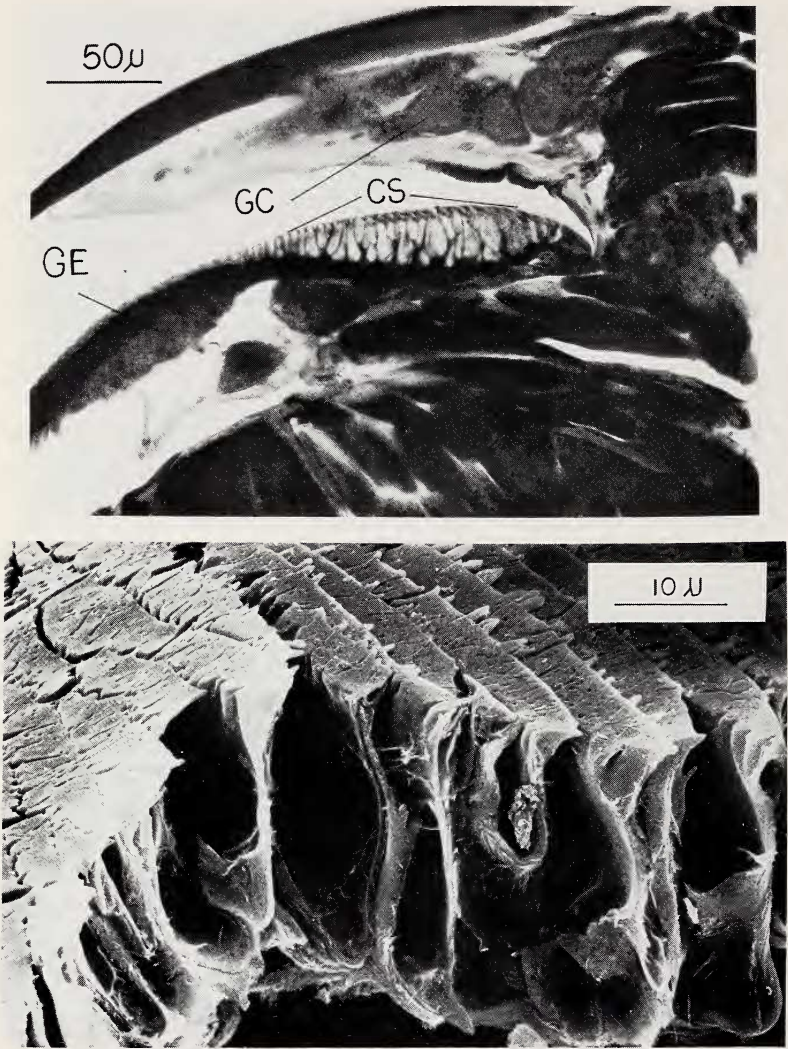


Figure 20. Above: Sagittal section through the pygidial gland of *Pachycondyla (=Termitopone) laevigata*. Below: SEM photograph of the cuticular structure (GA in Fig. 19) on 7th tergum. The cut open area shows the large cavities associated with the structure. (Lettering as in Fig. 5 and Fig. 18).



Figure 21. Sagittal section through the gaster of *Odontomachus haematoda*, showing the well developed reservoir of the pygidial gland (PG).

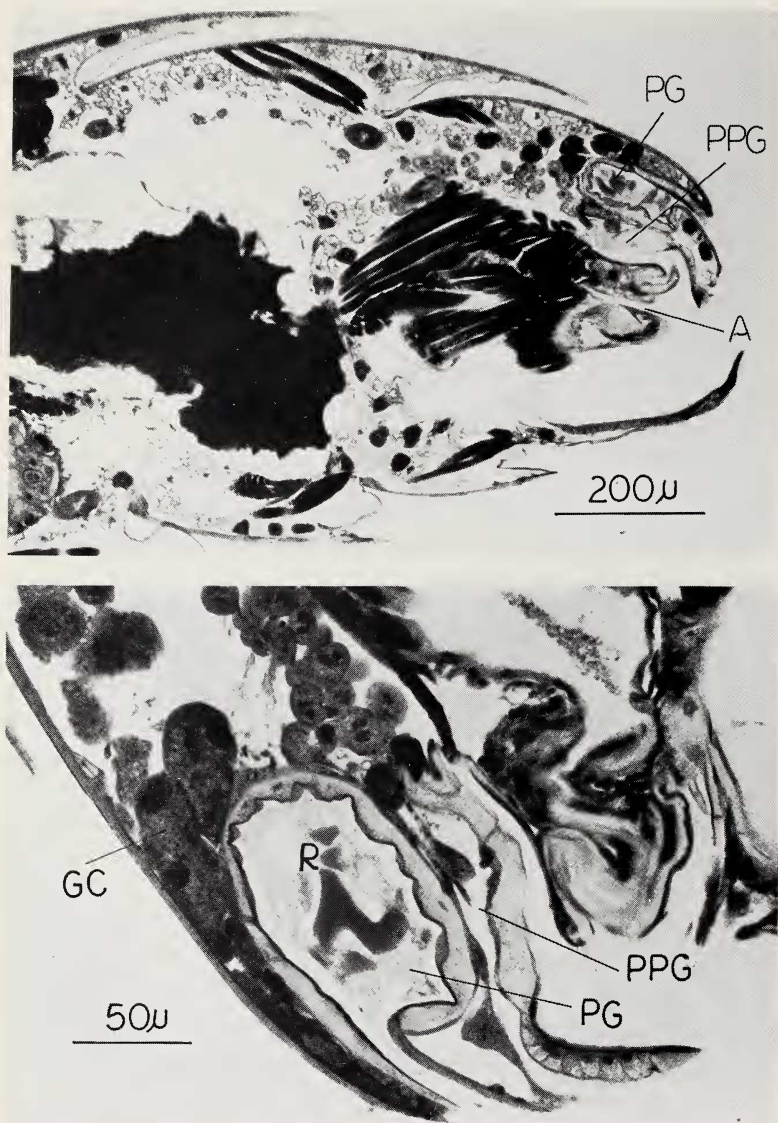


Figure 22. Above: Sagittal section through the gaster of *Neivamyrmex nigrescens*, showing the pygidial gland (PG), postpygidial gland (PPG) and anus (A). Below: Close up of sagittal section through pygidial gland and postpygidial gland of *N. nigrescens*. (Lettering as in Figs. 5 and 8; R = reservoir).

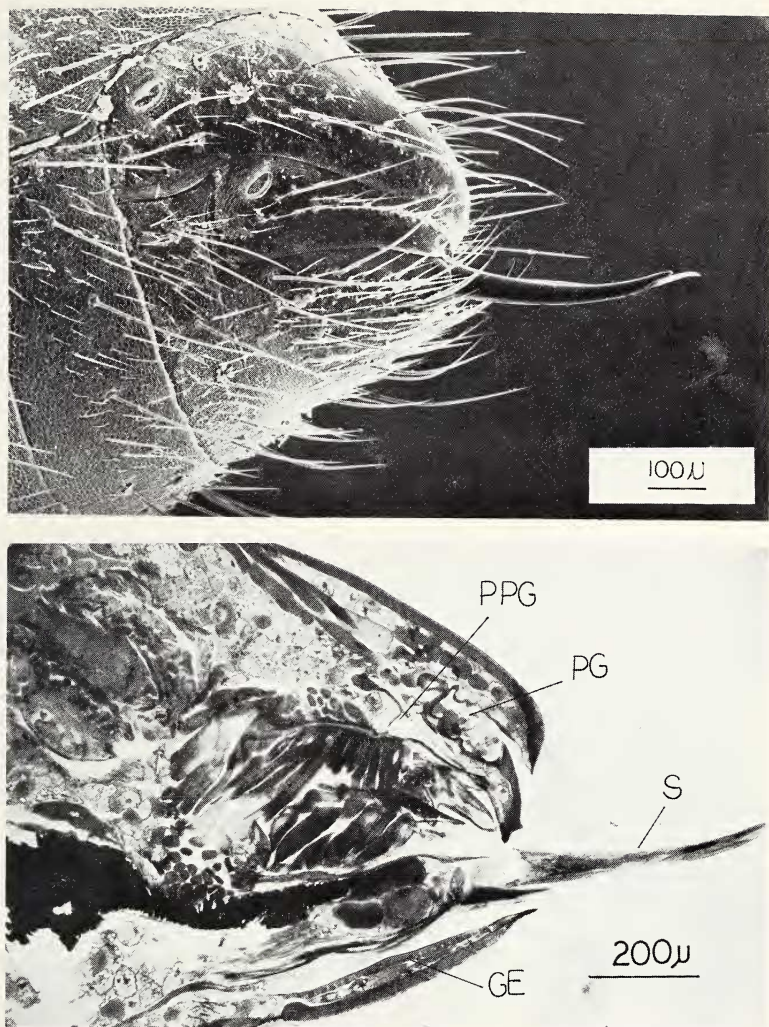


Figure 23. Above: SEM photograph of tip of the gaster of *Ecton hamatum*. Below: Sagittal section through the same segments. (Lettering as in Fig. 8; S = sting; GE = glandular epithelium in 7th sternum).

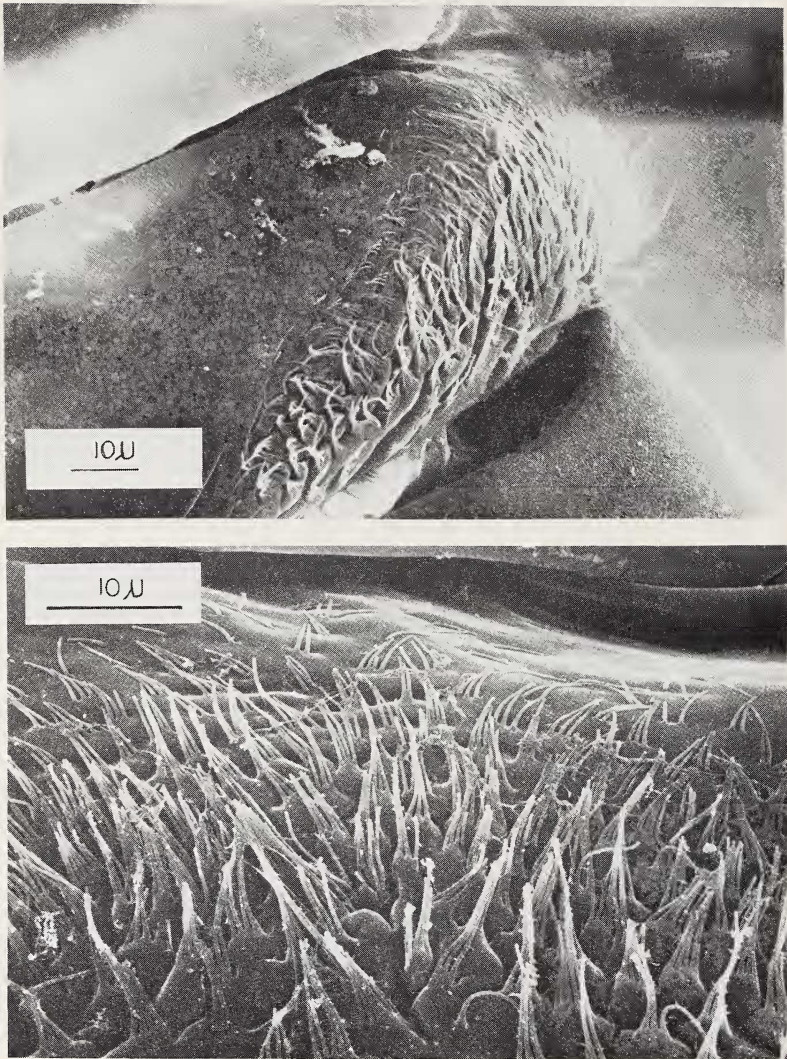


Figure 24. *Eciton hamatum*: SEM photograph of the intersegmental membrane between 6th and 7th terga, where the pygidial glands open. Below: Close up of the brush-like structure.

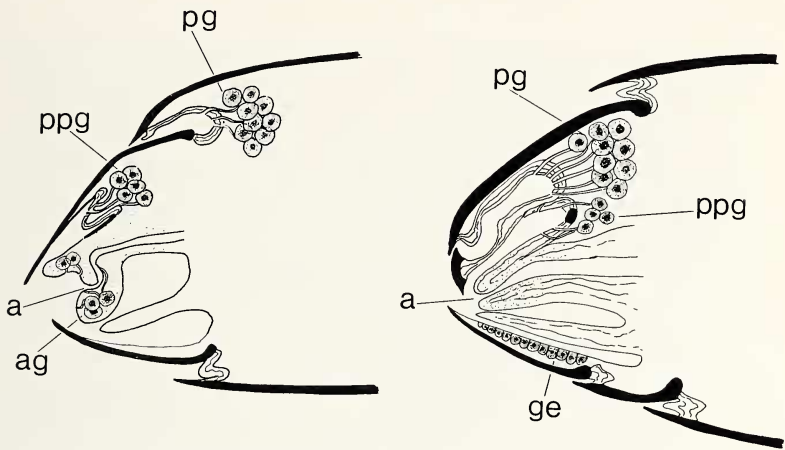


Figure 25. Schematic drawings of sagittal sections through the gaster tips of *Dorylus molesta* (left) and *Eciton hamatum* (right). (Lettering as in Fig. 8; a = anus; ag = anus glands).

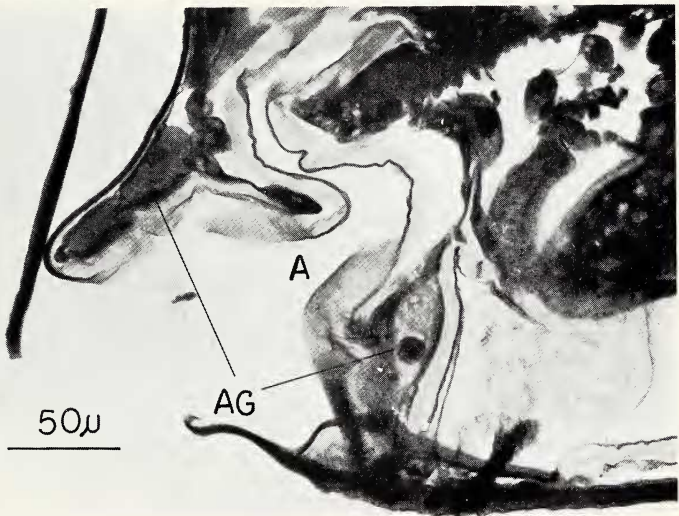


Figure 26. Sagittal section through anus of *Dorylus molesta* worker; AG = anus gland; A = anus.

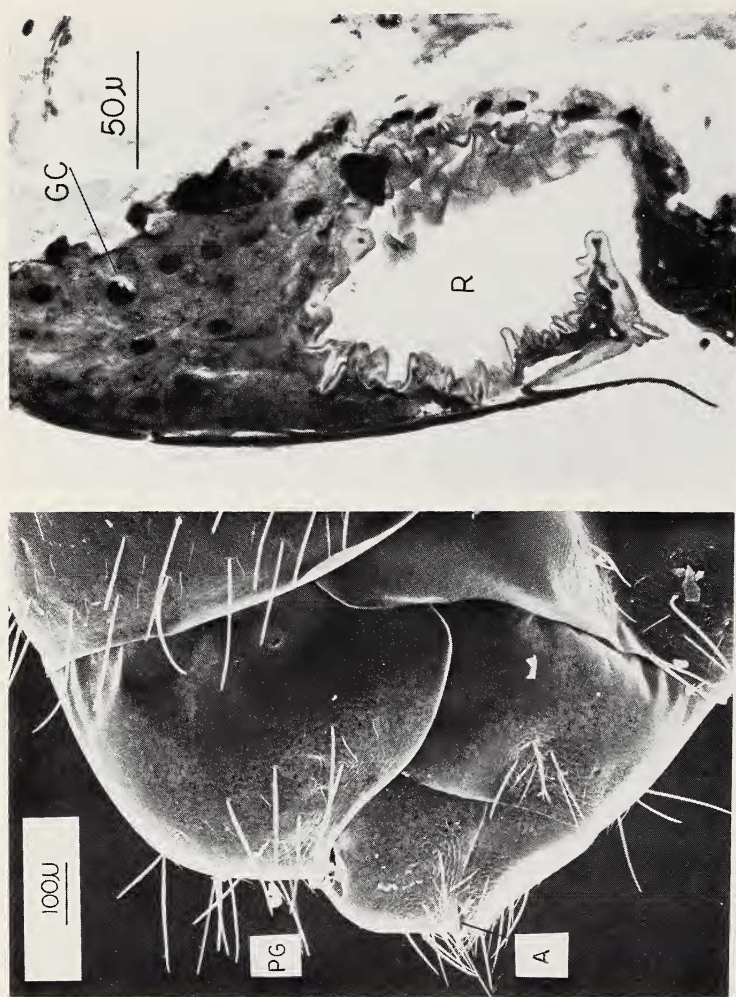


Figure 27. Left: SEM photograph of abdominal tip of *Veromessor pergandei*. "PG" indicates opening of pygidial gland between 6th and 7th terga; "A" indicates opening of anus. Right: Sagittal section through pygidial gland of *Veromessor*, which has a large reservoir (R) and each cell cluster contains 50–70 glandular cells (GC).

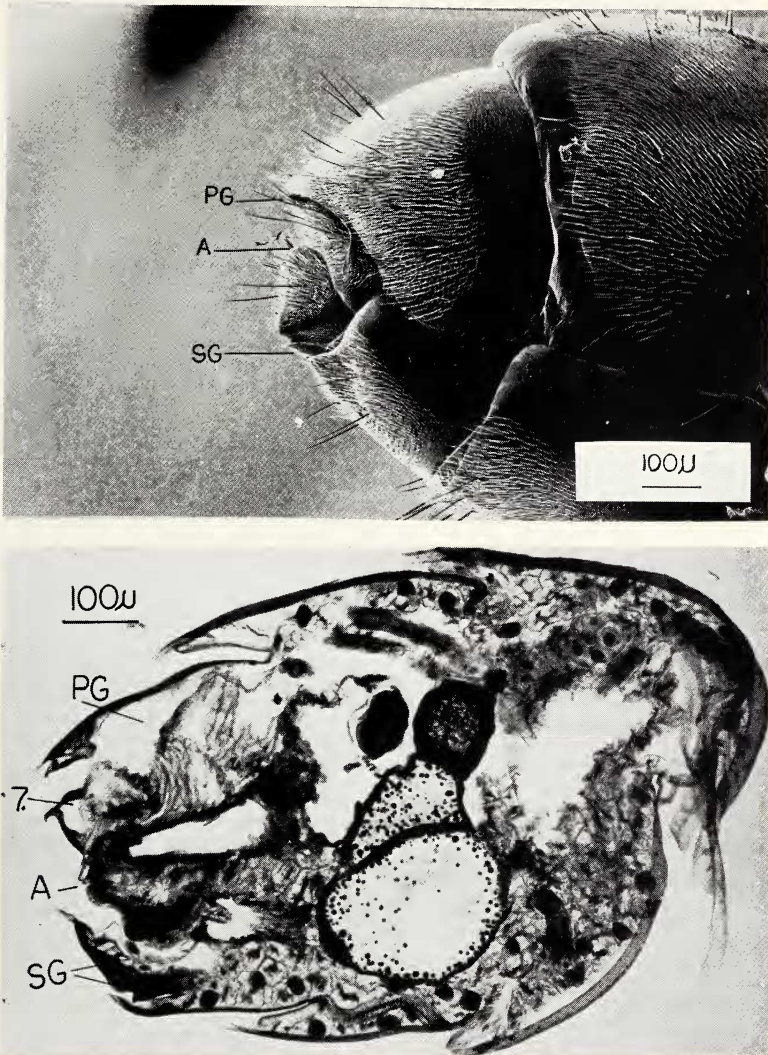


Figure 28. Above: SEM photograph of abdominal tip of *Liometopum apiculatum*. "PG" indicates where the pygidial gland opens between 6th and 7th terga. "A" indicates opening of anus; SG = sternal gland (Pavan's gland). Below: Sagittal section through gaster of *L. apiculatum*. PG = reservoir of pygidial gland; 7. = 7th tergum.

REFERENCES

- ALTENKIRCH, G.
1962. Untersuchungen über die Morphologie der abdominalen Hautdrüsen einheimischer Apiden (Insecta, Hymenoptera) Zoologische Beiträge, 7, 161-238.
- BERNSTEIN, R. A.
1974. Seasonal food abundance and foraging activity in some desert ants. The American Naturalist, 108, 490-498.
- BLUM, M. S.
1966. The source and specificity of trail pheromones in *Termitopone*, *Monomorium* and *Huberia*, and their relation to those of some other ants. Proceedings of the Royal Entomological Society of London, 41, 155-160.
1977. Behavioral responses of Hymenoptera to pheromones and allomones. Pp. 149-167 in Shorey, H. H. and J. J. McKelvey, Jr. (ed): Chemical control of insect behavior. John Wiley & Sons, New York 1977.
- BLUM, M. S. AND H. R. HERMANN.
1978a. Venoms and venom apparatuses of the Formicidae: Myrmeciinae, Ponerinae, Dorylinae, Pseudomyrmecinae, Myrmicinae and Formicinae. In: G. V. R. Born, O. Eichler, A. Farah, H. Heiken, A. D. Welch (ed). Handbook of Experimental Pharmacology, Springer-Verlag, Heidelberg 1978, pp. 801-869.
- BLUM, M. S. AND H. R. HERMANN.
1978b. Venoms and venom apparatuses of the Formicidae: Dolichoderinae and Aneuretinae. In: Handbook of Experimental Pharmacology, Springer-Verlag, pp. 871-894.
- BLUM, M. S. AND C. A. PORTOCARRERO.
1964. Chemical releasers of social behavior. IV. The hindgut as the source of the odor trail pheromone in the neotropical army ant genus *Eciton*. Ann. Entomol. Soc. America 57, 793-794.
- BORDAS, L.
1895. Appareil glandulaire des Hymenopteres. Ann. Sci. Nat. Zool. 19, 289-344.
- BROWN, C. A., J. F. WATKINS II AND D. W. ELDRIDGE.
1979. Depression of bacteria and fungi by the army ant secretion: Skatole. J. Kansas Entomol. Soc. 52, 119-122.
- CHADAB, R. AND C. RETTENMEYER.
1975. Mass recruitment by army ants. Science 188, 1124-1125.
- HÖLLDOBLER, B.
1978. Ethological aspects of chemical communication in ants. Advances in the Study of Behavior 8, 75-115.
- HÖLLDOBLER, B., M. MÖGLICH AND U. MASCHWITZ.
1973. *Bothroponera tesserinoda* (Formicidae): Tandemlauf beim Nestumzug. Encyclopaedia Cinematographica E 2040, pp. 3-14.
- HÖLLDOBLER, B., R. STANTON AND H. ENGEL.
1976. A new exocrine gland in *Novomessor* (Hymenoptera: Formicidae) and its possible significance as a taxonomic character. Psyche, 83, 32-41.

HÖLLDOBLER, B. AND C. P. HASKINS.

1977. Sexual calling behavior in primitive ants. *Science*, **195**, 793-794.

HÖLLDOBLER, B. AND E. O. WILSON.

1977. Weaver ants: Social establishment and maintenance of territory. *Science*, **195**, 900-902.

HÖLLDOBLER, B. AND E. O. WILSON.

1978. The multiple recruitment systems of the African weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* **3**, 19-60.

JANET, CH.

1898. Etudes sur les Fourmis, les Guépes et les Abeilles Note 17: Système glandulaire tégumentaire de la *Myrmica rubra*. Observations diverses sur les Fourmis. Paris, Georges Carré et C. Nand, Editeurs.

KOSCHEVNIKOV, G. A.

1899. Zur Kenntnis der Hautdrüsen der Apidae und Vespidae. *Anat. Anz.* **15**, 519-528.

KUGLER, CH.

1978. Pygidial glands in the myrmicine ants (Hymenoptera, Formicidae). *Insectes sociaux*, **25**, 267-274.

MASCHWITZ, U.

1964. Gefahrenalarmstoffe und Gefahrenalarmierung bei sozialen Hymenopteren. *Z. vergl. Physiol.* **47**, 596-655.

MASCHWITZ, U., B. HÖLLDOBLER AND M. MÖGLICH.

1974. Tandemlaufen als Rekrutierungsverhalten bei *Bothroponera tesserinoda* Forel (Formicidae: Ponerinae). *Z. Tierpsychol.* **35**, 113-123.

MASCHWITZ, U. AND W. KLOFT.

1971. Morphology and function of the venom apparatus of insects — bees, wasps, ants and caterpillars. *In: Venomous animals and their venoms* **3**, 1-60.

MASCHWITZ, U. AND P. SCHÖNEGGE.

1977. Recruitment gland of *Leptogenys chinensis*. *Naturwissenschaften*, **64**, 589-590.

PAVAN, M. AND G. RONCHETTI.

1955. Studi sulla morfologia esterna e anatomia interna dell'operaia di *Iridomyrmex humilis* Mayr e ricerche chimiche e biologiche sulla iridomirmecina. *Atti della Società Italiana di Scienze Naturali*, Milano, **94**, 379-477.

RATHMAYER, W.

1962. Methylmetacrylat als Einbettungsmedium für Insekten *Experientia* (Basel) **18**, 47-48.

1962. Das Paralyisierungsproblem beim Bienenwolf *Philanthus triangulum* F. (Hym. Sphec.) *Z. vergl. Physiol.* **45**, 413-462.

ROBERTSON, P. L.

1968. A morphological and functional study of the venom apparatus in representatives of some major groups of Hymenoptera. *Aust. J. Zool.* **16**, 133-166.

ROMEIS, B.

1948. *Mikroskopische Technik*. München 1948.

- TAYLOR, R. W.
1978. *Nothomyrmecia macrops*: A living-fossil ant rediscovered. *Science* **201**, 979-985.
- TOPOFF, H. AND J. MIRENDA.
1975. Trail-following by the army ant *Neivamyrmex nigrescens*: Responses by workers to volatile odors. *Ann. Entomol. Soc. Amer.* **68**, 1044-1046.
- WATKINS, J. F.
1964. Laboratory experiments on the trail following of army ants of the genus *Neivamyrmex* (Formicidae: Dorylinae). *J. Kansas Entomol. Soc.* **37**, 22-28.
- WATKINS, J. F., T. W. COLE AND R. S. BALDRIDGE.
1967. Laboratory studies on interspecific trail following and trail preference of army ants (Dorylinae). *J. Kansas Entomol. Soc.* **40**, 146-151.
- WATKINS, J. F., F. R. GEHLBACH AND J. C. KROLL.
1969. Attractant-repellent secretions in blind snakes (*Leptotyphlops dulcis*) and army ants (*Neivamyrmex nigrescens*). *Ecology* **50**, 1098-1102.
- WENT, F. W., J. WHEELER AND G. C. WHEELER.
1972. Feeding and digestion in some ants (*Veromessor* and *Manica*). *Bio-science* **22**, 82-88.
- WHEELER, J. AND S. W. RISSING.
1975. Natural history of *Veromessor pergandei* — II. Behavior. *The Pan-Pacific Entomologist* **51**, 303-314.
- WHELDEN, R. M.
1957. Notes on the anatomy of *Rhytidoponera convexa* Mayr ("violacea" Forel) (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Amer.* **50**, 271-282.
1957. Notes on the anatomy of the Formicidae I. *Stigmatomma pallipes* (Haldeman). *J. New York Entomol. Soc.* **65**, 1-21.
1960. The anatomy of *Rhytidoponera metallica* F. Smith (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Amer.* **53**, 793-808.
1963. The anatomy of adult queen and workers of the army ants *Eciton burchelli* Westwood and *Eciton hamatum* Fabricius. *New York Entomol. Soc.* **71**, 90-115.
- WILSON, E. O.
1971. *The insect societies*. The Belknap Press of Harvard University Press, Cambridge, Mass.